



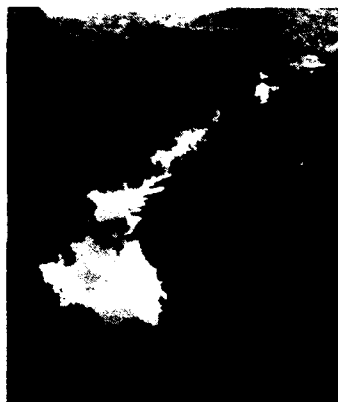
US Army Corps
of Engineers

ENVIRONMENTAL IMPACT
RESEARCH PROGRAM

MISCELLANEOUS PAPER EL-91-13

ROLE OF CHANNEL MIGRATION
IN THE INITIATION AND MAINTENANCE
OF FOREST COMMUNITIES
IN WESTERN TENNESSEE

AD-A236 661



by

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April 1991

Final Report

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91-01857



Prepared for DEPARTMENT OF THE ARMY
US Army Corps of Engineers
Washington, DC 20314-1000

Under Environmental Impact Research Program Work Unit 32391

Monitored by Environmental Laboratory
US Army Engineer Waterways Experiment Station
3909 Halls Ferry Road, Vicksburg, Mississippi 39180-6199

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REPORT DOCUMENTATION PAGE			Form Approved OMB No. 0704-0188	
<small>Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503.</small>				
1. AGENCY USE ONLY (Leave blank)	2. REPORT DATE April 1991	3. REPORT TYPE AND DATES COVERED Final report		
4. TITLE AND SUBTITLE Role of Channel Migration in the Initiation and Maintenance of Forest Communities in Western Tennessee		5. FUNDING NUMBERS WU 32391 C DACW39-89-M-3085		
6. AUTHOR(S) David Shankman				
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Department of Geography University of Alabama, Tuscaloosa Tuscaloosa, AL 35486		8. PERFORMING ORGANIZATION REPORT NUMBER		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) US Army Corps of Engineers, Washington, DC 20314-1000 USAEWES, Environmental Laboratory, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199		10. SPONSORING/MONITORING AGENCY REPORT NUMBER Miscellaneous Paper EL-91-13		
11. SUPPLEMENTARY NOTES Available from National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161				
12a. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution unlimited			12b. DISTRIBUTION CODE	
13. ABSTRACT (Maximum 200 words) Forest regeneration was examined on abandoned channels and newly created point bars along the Hatchie River in western Tennessee. Tree age and size data are used to reconstruct the development of the young forest stands and to predict future changes. New point bar surfaces favor the establishment of <i>Acer saccharinum</i> and, to a lesser extent, <i>Salix nigra</i> and <i>Populus deltoides</i> . <i>Taxodium distichum</i> and <i>S. nigra</i> are the first species to colonize oxbow lakes after the channel cuts off. Longevity of the early colonizers is highly variable. <i>S. nigra</i> is short-lived, whereas <i>T. distichum</i> may dominate a site for more than 500 years. However, densities of all pioneer species on both abandoned channels and point bars decline with increasing age of the surface. With the exception of <i>A. saccharinum</i> , these species have low reproductive success in mature stands and will be replaced by shade-tolerant species that establish much later. Therefore, the early colonizers rarely occur on older surfaces. Channel movement and the creation of new surfaces will maintain these species in the lower bottomlands of undisturbed streams. However, the initiation of pioneer communities may be precluded in some areas by stream channelization and bank stabilization. Maintaining straightened channels prevents the formation of oxbows and point bars. Therefore, the primary regeneration surfaces for many species no longer exist.				
14. SUBJECT TERMS Biodiversity Stream stabilization Riparian forest			15. NUMBER OF PAGES 25	
			16. PRICE CODE	
17. SECURITY CLASSIFICATION OF REPORT UNCLASSIFIED	18. SECURITY CLASSIFICATION OF THIS PAGE UNCLASSIFIED	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT	

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Preface

This work was sponsored by Headquarters, US Army Corps of Engineers (HQUSACE), as part of the Environmental Impact Research Program (EIRP), Work Unit 32391. Additional support was provided by the University of Alabama (UA), Research Grants Committee. The Technical Monitors for the EIRP were Dr. John Bushman, Mr. David Buelow, and Mr. Dave Mathis, all with HQUSACE.

This report was prepared for the US Army Engineer Waterways Experiment Station (WES) by Dr. David Shankman, Department of Geography, UA, Tuscaloosa, under Contract No. DACW-39-89-M-3085. Dr. Charles Klimas, Wetland and Terrestrial Habitat Group (WTHG), Environmental Laboratory (EL), WES, was the study manager.

Mr. David A. Bell and Ms. Laurel G. Drake (UA) assisted with the research, and Mr. James W. Teaford, Mr. Hollis H. Allen, and Dr. Klimas (WTHG) reviewed the manuscript. The report was prepared under the general supervision of Mr. Edward C. Brown, Chief, WTHG; Dr. Conrad J. Kirby, Chief, Environmental Resources Division, EL; and Dr. John Harrison, Chief, EL. Dr. Roger T. Saucier was the Program Manager. The report was edited by Ms. Janean C. Shirley of the Information Technology Laboratory, WES. Figures were prepared by the UA Cartographic Research Laboratory.

Commander and Director of WES during this study was COL Larry B. Fulton, EN. Technical Director was Dr. Robert W. Whalin.

This report should be cited as follows:

Shankman, David. 1991. Role of Channel Migration in the Initiation and Maintenance of Forest Communities in Western Tennessee. Miscellaneous Paper EL-91-13, Vicksburg, MS: US Army Engineer Waterways Experiment Station.

1 Introduction

Riparian ecosystem management issues in the Southeastern United States differ from those usually cited in other parts of the country. Most riparian zones are regarded as fairly narrow corridors along streams, and the habitat values associated with them relate to the presence of particular vegetation types in direct proximity to a watercourse. Thus, in mountainous terrain, riparian forests are valued for the shading, organic inputs, and sediment control they provide to cold-water streams; in arid regions, the presence of a highly productive, multi-layered plant community in association with free water provides an essential habitat element for most resident and migratory wildlife (Brinson et al. 1981). Along alluvial rivers of the Southeast, however, the habitat values attributed to riparian forest are derived from a broader zone of streamside terrain which encompasses the entire active floodplain. It is the remarkable diversity within and among plant communities, the high productivity, and the differential seasonal flooding of those forests, that are the foundations of the wildlife habitat base (Fredrickson 1978). Riparian zone management issues in this ecosystem focus on the mechanisms that maintain the intrinsic habitat quality of particular forest communities, and the interspersions of diverse habitat types throughout the floodplain.

One activity that generally works against maintenance of a complex and dynamic floodplain ecosystem is stream stabilization. Establishment of a stable, efficient stream

channel is a common objective of flood control and navigation projects in the Southeastern United States. It is often accomplished through channelization and bank stabilization. The recognized environmental impacts of such efforts may include the loss or modification of certain aquatic and terrestrial habitats, and changes in the timing and duration of forest flooding, which are important to a variety of fish and wildlife species (Wharton et al. 1982). An important indirect impact on habitat quality has been reported in association with stabilization of the Mississippi River (Johnson 1973; Klimas 1988), but generally has gone unrecognized with regard to other alluvial streams in the Southeast. This concerns the effects of arresting a geological process, stream meandering, which in turn controls habitat diversity on a long-term, basin-wide scale.

Floodplains are among the most rapidly changing geomorphic surfaces. Erosion and deposition of the streambed and bottomland surfaces result in channel migration, avulsion, and abandonment, in addition to a variety of microtopographic features. Several studies have found channel migration to be the major determinant of vegetation patterns in many alluvial habitats (Shelford 1954; Salo et al. 1978; Kalliola and Puhakka 1988). Along meandering streams, deposition on the inside of channel bends creates new surfaces, point bars, that favor the establishment of species requiring exposed sites and high light levels for successful col-

onization (Shelford 1954; Johnson, Burgess, and Keammerer 1976; Noble 1979; Bradley and Smith 1986). Lengthy periods of deposition result in progressively older forest stands with increasing distance from the active channel (Everitt 1968; Viereck 1970; Hickin and Nanson 1975; Nanson and Beach 1977). The curvature of the channel bend increases, eventually coming together to form a cutoff. The active channel then changes course, leaving an oxbow lake. There has been little research on oxbow succession. However, in the classic succession model of a hydrarch sere, the filling of a lake by sediment and organic debris produces a sequence of plant communities which are eventually dominated by forest vegetation. The terrestrial vegetation initially establishes at the lake margins and later appears in a series of zones closer to the interior as new surfaces are exposed (Clements 1916). The composition of early forest communities in abandoned meanders is limited by lengthy periods of inundation during the growing season, which exclude species that are not highly flood tolerant.

The rapid rates of channel migration in the broad alluvial valleys of the Southeastern Coastal Plain create complex patterns of abandoned meanders and point bar deposits. This process results in a mosaic of distinct forest communities with the com-

position depending on the stage of geomorphic development. However, many Coastal Plain streams have been channelized. The maintenance of a straightened channel excludes the formation of point bars and oxbow lakes. Therefore, the largest scale natural disturbance mechanism and the most important factor controlling spatial heterogeneity in the lower bottomland sites has been eliminated. Knowledge of forest development initiated through this process is essential in order to understand how channelization will affect the future development of bottomland forest communities. However, the development of terrestrial vegetation on new surfaces created by channel migration in the Southeastern Coastal Plain has been given little attention. Documentation of plant community development processes on these sites (point bars and abandoned channels) can provide an indication of the rate at which certain communities might be expected to disappear from the floodplain forest following stream stabilization. Riparian ecosystem management plans can better incorporate long-term diversity considerations if this process is recognized and described. This study is intended to provide information for a particular reach of the relatively unaltered Hatchie River in west Tennessee, which may serve as a general model for other alluvial systems in the region.

2 Study Area

The Hatchie River floodplain was selected for study because of the absence of channel construction common on most of the large streams in this region. It is a low-gradient, meandering stream that has dissected a loess-covered plateau, creating a floodplain typically 3 to 5 km wide that is bounded by late Pleistocene terraces (Saucier 1987). On the lower bottomland sites are complex patterns of abandoned meanders. The alluvium of the active floodplain consists of eroded loess and sediments from underlying Coastal Plain formations. The Hatchie River drainage basin area is about 6,080 km². Average discharge between 1970 and 1988 was 91 m³/sec (US Army Corps of Engineers, multiple years).

As a consequence of rapid channel migration and variable inundation regimes, the lower bottomlands of the Hatchie River are composed of a mosaic of distinct forest communities. Small variations in surface topography affect soil moisture conditions, and therefore often influence plant communities

on a fine scale. However, the larger scale geomorphic features, abandoned meanders and point bars, are the basic determinants of community composition. *Acer saccharinum* (silver maple) and *Salix nigra* (black willow) typically establish on newly formed point bar surfaces. *Taxodium distichum* (baldcypress), which often exceeds 40 m in height and 1.5 m in diameter, is the most common tree on abandoned channels and sloughs. Older point bar surfaces and meander scars that hold water for only short periods also support *Carya aquatica* (water hickory), *Fraxinus pennsylvanica* (green ash), and *Gleditsia aquatica* (water locust). Common understory species on frequently inundated sites include *Planera aquatica* (water elm) and *Forestiera acuminata* (swamp privet). Most of these species occur infrequently on older, higher surfaces that are dominated by less flood-tolerant species that may extend to the floodplain margins. (Botanical nomenclature follows Radford, Ahles, and Bell (1968).)

3 Methods

Study sites on abandoned meanders and point bars were located in a 5-km² area of the Lower Hatchie National Wildlife Refuge, which is approximately 12 km above the junction of the Hatchie and Mississippi Rivers (Figure 1). This is one of the few forested areas in the floodplain that has not been extensively logged, and is one of the few areas in the region that supports baldcypress stands with individuals several centuries old.

Abandoned Channels

Eight study sites were established in meander scars (Table 1). The study sites represent a range of ages (200-400 years), or time since cut-off, of meander scars, as indicated by the slope and height of the former channel banks and current periods of inundation during the growing season. Shortly after cut-off, the abandoned channels

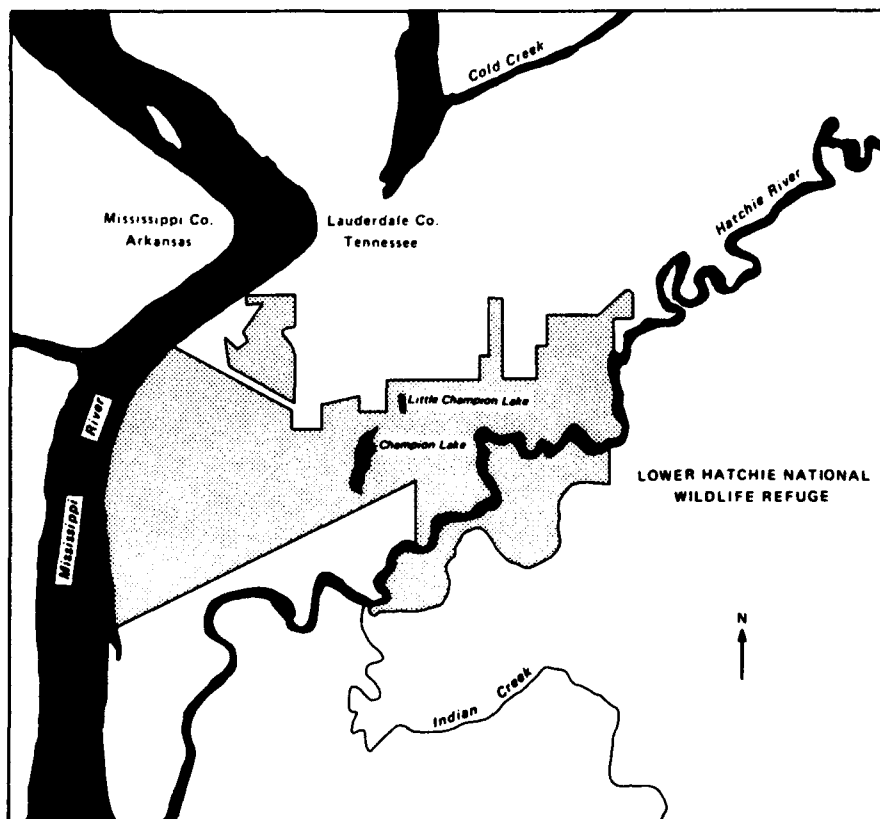


Figure 1. Map showing location of the Lower Hatchie National Wildlife Refuge

Table 1
 Characteristics of Meander Scar Stands in the Lower Hatchie National Wildlife Refuge

	Sites							
	1	2	3	4	5	6	7	8
Plot size (m ²)	1,280	1,520	1,200	3,040	1,936	3,240	2,400	2,040
Density (stems \geq 4 cm diameter/ha)								
<i>Taxodium</i>	156	144	83	62	108	86	54	25
<i>Salix</i>	23	33	58					
<i>Gleditsia</i>	55		42	56				
<i>Acer</i>	31		83	114	62	176	129	74
<i>Fraxinus</i>	31			32	26	34	62	29
<i>Carya</i>				7			17	15
<i>Quercus</i>				10			10	
<i>Planera</i>	23	99	158	52	21	137	83	
<i>Forestiera</i>	47		33	95	26	34	21	74
<i>Celtis</i>						9	62	103
Total	366	276	457	428	243	339	492	403
Basal area (m ² /ha)								
<i>Taxodium</i>	53	50	31	51	102	66	26	19
<i>Salix</i>	5	6	11					
<i>Gleditsia</i>	3		2	4				
<i>Acer</i>	2		1	4	1	7	4	8
<i>Fraxinus</i>	<1			12	2	<1	4	3
<i>Carya</i>				<1			4	2
<i>Quercus</i>				<1			2	
<i>Planera</i>	<1	4	3	<1	<1	2	1	
<i>Forestiera</i>	<1		<1	<1	<1	<1	<1	<1
<i>Celtis</i>						<1	<1	1

are deeply incised and typically hold water for long periods of time each year. Over-bank deposition and the absence of continuous scouring that occurs in the active channel results in rapid vertical accretion and progressively shorter periods of inundation. Sites 1, 2, and 3 typically remain under water well into May or early June, several weeks longer than sites 4, 5, and 6. Sites 7 and 8 are under water only a short period of time beyond that of the surrounding older surfaces. Boundaries were established at the bottom of the former channel banks. Perpendicular boundaries were established

so that the study sites excluded areas where there was evidence of recent logging or other human disturbances. Study sites varied in size from 0.12-0.32 ha (Table 1).

Tree diameters were measured at the 1.4-m height of individuals \geq 4 cm in diameter, except for baldcypress, which were measured at the 2-m height because their fluted buttresses prevented meaningful comparisons of size nearer the ground. Diameter data were used to calculate dominance, and the vertical stand structure was characterized by classifying all trees as canopy domi-

nant, codominant, or subcanopy. All trees ≥ 4 cm in diameter were cored with an increment borer to determine approximate age. Sediment deposition in the oxbows buries the base of trees, with the distance between the ground and the germination surface depending on the age of the tree and rates of sedimentation. Baldcypress is the earliest surviving colonizer in the older stands.

Therefore, the coring position on these sites is well above the germination surface. However, young baldcypress grow rapidly on exposed sites (Demaree 1932). Therefore, the time required for a first-year seedling to reach coring height is a small percentage of the reported ages. Stem diameter was used as an indicator of relative age for many large baldcypress because interior rotting prevented the counting of annual rings on the collected cores. Linear and log-transformed regressions and Pearson correlation analysis were used to determine diameter-age relationships. However, in some stands there were not enough individuals in a population to allow regression analysis.

The spatial distribution of trees was determined by mapping all individuals ≥ 4 cm in diameter in 2- by 2-m contiguous quadrats in each of the study sites. An exact

probability test was used to determine if the proximity of the individuals to the former channel banks departed from a random distribution (Appendix A).

Point Bars

New point bar surfaces created by deposition on the convex side of meanders are rapidly colonized by trees. Therefore, surface age increases with distance from the channel. On four actively migrating point bars, transects were located perpendicular to the channel. Each transect was 20 m wide and between 80 and 170 m in length. The transects were divided into 20-m-wide segments for sampling of progressively older surfaces. All trees within each 20- by 20-m plot were measured by diameter as on the meander scar study sites. The oldest trees were used as an indicator of surface age (cf. Everitt 1968; Hicken and Nanson 1975). On the longest point bar transect, the oldest trees, based on size and bark characteristics, were cored at the 1.4-m height to determine age. Approximately three trees from each transect plot were cored.

4 Results

Abandoned Channels

The forest stands in meander scars were dominated by large baldcypress, which in many cases exceeded 30 m in height and 1 m in diameter. Most were classified as canopy dominant. Baldcypress basal area ranged from 19 to 102 m²/ha (Table 1). The lack of regeneration along the active channel of the lower Hatchie River indicates these stands initially established after the channel cut-off and creation of an oxbow lake. Maximum baldcypress ages on each site, as determined from cores, ranged from 190 to 277 years (Table 2). However, most individuals > 1 m in diameter (mostly on sites 4, 5, and 6) were not aged because of rot. Regression analysis reveals moderate to strong diameter-age relationships (Table 3). The average diameter growth rates were .33-.39 cm/yr and had low coefficients of variation. Assuming the largest baldcypress maintained similar growth rates as the oldest aged trees, baldcypress greater than 1.5 m in diameter would be more than 400 years old.

Black willow was codominant on the younger sites (1,2,3) and all individuals were classified as canopy dominants. Few were aged because of rotted centers and large, dead individuals were common. No black willow occurred in the older stands. Other species occasionally occupying codominant canopy positions were green ash, water hickory, water locust, and silver maple. The proportional dominance of

these species varied among stands. On sites 1, 2, and 3; the relative dominance for each never exceeded 5 percent, but was considerably higher on some of the older stands (Table 1). The most common understory species were swamp privet and water elm.

Baldcypress regeneration was discontinuous on all stands. First year baldcypress seedlings were common. However, the absence of intermediate-aged individuals indicates infrequent seedling survival. Only two individuals were aged at less than 100 years and both occurred on the interior of relatively young sites on which a dense forest canopy had not yet developed (sites 1 and 2) (Table 4). These individuals may represent the initiation of a second pulse of regeneration which is evident on the interior of the older sites. Regardless, the regeneration rates in these stands will not maintain the older populations. There was no evidence of regeneration on any of the older sites or on the margins of the young sites where there was a well-developed forest canopy, suggesting that baldcypress is highly shade intolerant.

The general lack of young black willow and its absence on the older study sites and surrounding surfaces indicate that initial colonizers are short-lived and that regeneration is discontinuous. Therefore, black willow is present in abandoned meanders only a few decades after meander cutoffs. The successful colonization by the other codominant species began at least several decades after the cessa-

Table 2
Summary of Ages and Diameter (cm) at 1.4-m Height (*Taxodium*, 2-m Height)
for Each Species, Arranged by Site

Site and Species	N (n aged)	Diameter		Age	
		Median	Range	Median	Range
Site 1					
<i>Taxodium</i>	20 (18)	63	26-114	182	92-220
<i>Salix</i>	3 (2)	56	44-60	81	81
<i>Gleditsia</i>	7 (7)	20	10-46	53	47-97
<i>Acer</i>	4 (3)	22	19-51	45	43-52
<i>Planera</i>	3 (2)	21	11-31	61	61
<i>Fraxinus</i>	4 (4)	14	14-16	40	33-50
<i>Forestiera</i>	6 (6)	9	7-17	36	23-52
Site 2					
<i>Taxodium</i>	22 (14)	66	37-97	205	160-244
<i>Salix</i>	5 (0)	50	24-69		
<i>Planera</i>	15 (10)	21	12-34	67	30-87
Site 3					
<i>Taxodium</i>	10 (9)	70	13-95	185	59-225
<i>Salix</i>	7 (2)	50	29-65		
<i>Planera</i>	19 (19)	14	8-23	51	33-96
<i>Gleditsia</i>	5 (5)	23	15-33	69	60-119
<i>Acer</i>	10 (9)	11	8-20	38	28-57
<i>Forestiera</i>	4 (4)	9	6-12	45	25-75
Site 4					
<i>Taxodium</i>	19 (6)	97	51-175	225	202-250
<i>Acer</i>	35 (33)	17	8-73	42	24-114
<i>Planera</i>	16 (16)	13	9-19	49	27-86
<i>Forestiera</i>	29 (25)	10	5-19	32	21-52
<i>Gleditsia</i>	17 (15)	30	21-44	80	36-108
<i>Carya</i>	2 (2)	12	7-18	58	30-86
<i>Quercus</i>	3 (3)	12	7-18	31	24-37
<i>Fraxinus</i>	10 (10)	68	49-87	31	17-57
Site 5					
<i>Taxodium</i>	21 (8)	99	33-192	225	165-277
<i>Acer</i>	12 (8)	15	11-23	35	25-48
<i>Planera</i>	4 (4)	24	14-33	45	30-61
<i>Forestiera</i>	5 (5)	7	6-13	34	22-51
<i>Fraxinus</i>	5 (4)	30	13-47	46	26-62

(Continued)

Table 2 (Concluded)

Site and Species	N (n aged)	Diameter		Age	
		Median	Range	Median	Range
Site 6					
<i>Taxodium</i>	28 (14)	86	31-184	195	115-259
<i>Acer</i>	57 (48)	14	7-37	41	23-112
<i>Fraxinus</i>	11 (10)	16	9-21	76	33-118
<i>Forestiera</i>	11 (9)	9	7-12	34	21-59
<i>Celtis</i>	3(3)	11	9-14	33	31-38
Site 7					
<i>Taxodium</i>	13 (10)	69	42-142	164	125-190
<i>Fraxinus</i>	15 (12)	22	15-58	51	27-60
<i>Acer</i>	31 (21)	14	8-68	34	19-58
<i>Carya</i>	4 (1)	48	41-69	152	
<i>Quercus</i>	2 (0)	56	44-68		
<i>Planera</i>	33 (28)	10	4-24	29	13-77
<i>Celtis</i>	15 (13)	10	4-16	28	16-54
<i>Forestiera</i>	5 (2)	7	6-9	28	27-30
Site 8					
<i>Taxodium</i>	5 (2)	99	78-140	191	163-220
<i>Acer</i>	15 (10)	32	10-69	52	21-110
<i>Planera</i>	17 (16)	13	7-26	29	16-65
<i>Forestiera</i>	15 (13)	9	5-18	27	18-53
<i>Carya</i>	3 (2)	37	19-62	62	48-76
<i>Celtis</i>	21 (17)	11	5-18	27	16-38

Table 3

Diameter-Age Relationships of *Taxodium* and Average Rates of Diameter Growth (cm/yr)
 \pm Standard Deviation on Sites Where $n \geq 10^*$

Study Sites	n	r	Regression Equation	Significance	Diameter Growth
1	18	.80	$Y = -126.5 + 74.8 \log eX$	<0.01	$.33 \pm .06$
2	14	.67	$Y = -109.9 + 75.9 \log eX$	<0.01	$.31 \pm .06$
6	14	.88	$Y = 62.0 + 1.9 X$	<0.01	$.33 \pm .05$
7	10	.66	$Y = -70.5 + 56.3 \log eX$	<0.05	$.39 \pm .05$

* Y is years and X is cm diameter at 2-m height. Significance is based on the F-test of linear and log-transformed regressions.

Table 4
Age-Class Distributions of Trees/ha in Abandoned Channels in the
Lower Hatchie National Wildlife Refuge*

	Age Classes											
	1	2	3	4	5	6	7	8	9	10	11	12
Site 1												
<i>Taxodium</i>					8		32	24	55	16	8	
<i>Salix</i>				8								
<i>Gleditsia</i>		32	16	8								
<i>Fraxinus</i>	16	16										
<i>Acer</i>		24										
<i>Planera</i>			16									
<i>Forestiera</i>	48											
Site 2												
<i>Taxodium</i>								26	10	15	10	10
<i>Planera</i>	20	20	10									
Site 3												
<i>Taxodium</i>		8				8		17	17	8	17	
<i>Gleditsia</i>			24	8	8							
<i>Planera</i>	24	92	33	8								
<i>Forestiera</i>	17	88										
<i>Acer</i>	40	33										
Site 4												
<i>Taxodium</i>										10	3	7
<i>Gleditsia</i>	3		23	20	3							
<i>Acer</i>	59	39	7		3							
<i>Planera</i>	23	20	3		7							
<i>Carya</i>	3			3								
<i>Fraxinus</i>	23		10									
<i>Forestiera</i>	72	10										
<i>Quercus</i>	10											
Site 5												
<i>Taxodium</i>								5		15	5	15
<i>Fraxinus</i>	5	10	5									
<i>Planera</i>	10	5	5									
<i>Acer</i>	26	15										
<i>Forestiera</i>	15	10										

(Continued)

* The age classes are: 1, less than 40 years; 2-11, 20-year increments beginning at 40 years; 12, > 240 years.

Table 4 (Concluded)

	Age Classes											
	1	2	3	4	5	6	7	8	9	10	11	12
Site 6												
<i>Taxodium</i>					3		6	6	6	6	12	3
<i>Fraxinus</i>	3	3	12	9	3							
<i>Acer</i>	65	65	12	3	3							
<i>Forestiera</i>	22	6										
<i>Celtis</i>	9											
Site 7												
<i>Taxodium</i>						8	13	8	13			
<i>Carya</i>							4					
<i>Fraxinus</i>	4	42	4									
<i>Acer</i>	4	62	21									
<i>Planera</i>	104	8	4									
<i>Celtis</i>	50	4										
<i>Forestiera</i>	8											
Site 8												
<i>Taxodium</i>								1		1		
<i>Acer</i>	15	25		5	5							
<i>Fraxinus</i>		20	10									
<i>Carya</i>		5	5									
<i>Planera</i>	96	5	5									
<i>Forestiera</i>	59	5										
<i>Celtis</i>	83											

tion of baldcypress regeneration. Both silver maple and green ash were absent from some of the young stands. However, their age-class distributions on the older sites indicate continuous regeneration after initial establishment (Table 4). Occasional maple-ash codominance demonstrates their size-class recruitment in a baldcypress understory. Water elm and swamp privet were well represented among the young age classes. Both are short-lived and typically become reproductively mature without emerging into the canopy. *Celtis laevigata* (sugarberry) was also represented in the youngest age classes, but occurred only in the older stands.

The spatial distributions of baldcypress size classes indicate that, in most cases, colonization begins at the edges of the oxbow and later establishes in the interior (Table 5). On the younger sites (1,2,3) most baldcypress occurred near the former channel banks where even small seasonal water level fluctuations expose surfaces, which is necessary for germination (Figure 2a). On the older sites most individuals in the large size classes were found near the former banks, a pattern congruent with the younger stands (Figure 2b). In contrast, the younger individuals on these sites were typically clustered toward the interior of the channel. These individuals established on new

Table 5

Probability of Random Channel Bank or Interior Clustering of Observed Distributions of *Taxodium**

Study Sites	<u>1</u>	<u>2</u>	<u>3</u>	
Small**	.0004 (19)	.00003 (23)	.006 (10)	
Study Sites	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>
Small †	.005 (12)	.01 (12)	.00001 (19)	.07 (11)
Large**	.001 (6)	.006 (9)	.0005 (10)	-

* Trees are categorized in two size classes: < 1 m diameter (small) and > 1 m diameter (large). Number of individuals are in parentheses.

** Probability that the observed distribution or a distribution closer to the channel bank occurred randomly.

† Probability that the observed distribution or a distribution closer to the channel center occurred randomly.

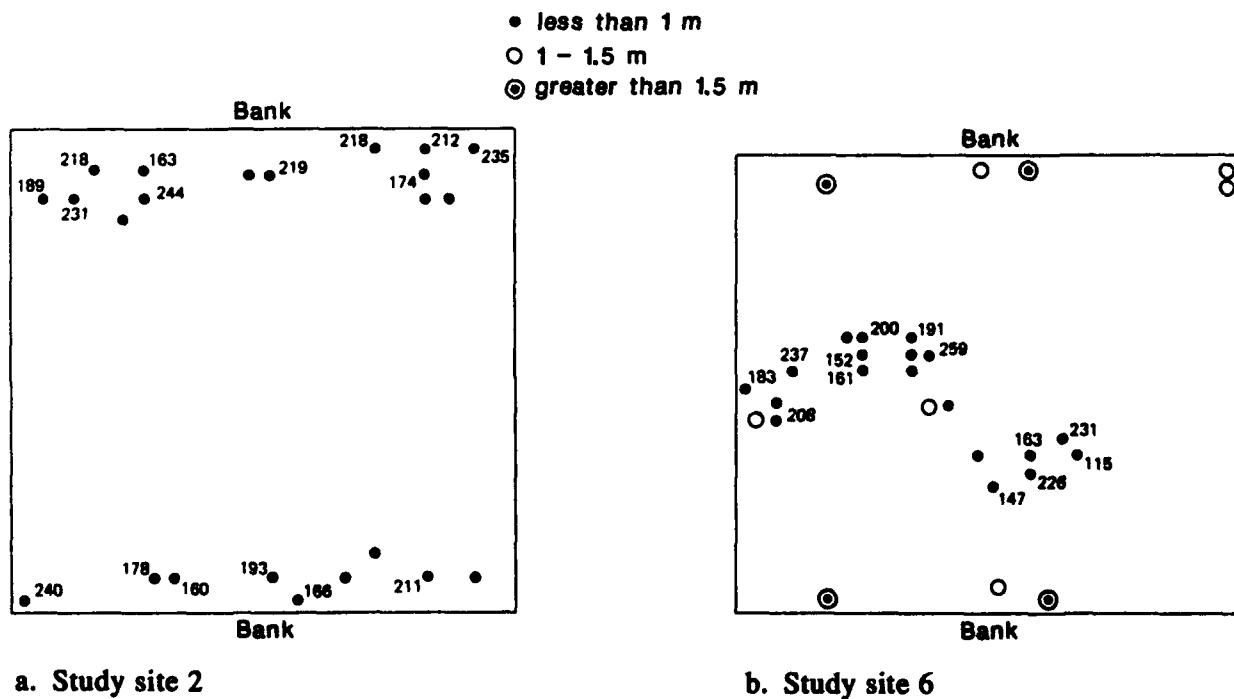


Figure 2. Maps of study sites 2 and 6 showing size of cypress (diameter at 2-m height) and location relative to the former channel banks. Ages (in years) are also shown. Study sites are not shown at the same scale

surfaces as the lake filled in. The estimated ages of the largest individuals occurring on sites 4, 5, and 6 were greater than 400 years. Discontinuous regeneration after canopy development indicates that these are initial cohorts that established at the lake margins. The difference in maximum age of the oldest individuals at the meander margins and those in the interior (250-277 years), is greater than 150 years. Therefore, colonization in the interior of the former oxbow may begin more than one and possibly two centuries after initial baldcypress colonization at the oxbow margins. The time between the two colonization periods depends primarily on rates of sedimentation. The exceptions in these spatial patterns are sites 7 and 8, in which few individuals occurred.

Initial spatial patterns of black willow may have been similar to those of baldcypress. However, black willow is short-lived and too few individuals remain, even on the youngest sites, to evaluate its spatial distribution at the earlier stages of stand development. The other species initially colonized after deposition raised surfaces and reduced flooding frequency and duration. Therefore, inundation of the interior of the site, which strongly influenced baldcypress inter-stand distributions, appears to have had a minor effect on the spatial patterns of later colonizers.

Point Bars

Successful establishment of silver maple, black willow, and *Populus deltoides* (cottonwood) occurs primarily on recently created point bar surfaces. The age of individuals along the transect that established adjacent to the channel indicates average channel movement at maximum curvature to be 0.58 m/year ($s = .15$) during the last 100 years. Assuming similar climatic conditions during the past 200 to 300 years, the rates of erosion and deposition, which are deter-

mined by discharge, were somewhat constant. However, rates of localized deposition depend on channel configuration. Along gentle bends, bank erosion and sedimentation are slow. As the curvature of the bends increases, point bar development accelerates. Therefore, it is not assumed that the rate of deposition of each point bar is constant.

Silver maple is the most common early colonizer on newly formed Hatchie River point bars. Densities on the youngest surface plots (0-20 m) ranged from 1,600-2,475 stems/ha (Table 6). Silver maple dominated surfaces less than 100 years old. However, its reproductive success was limited on older surfaces. Silver maple density declined rapidly with distance from the channel, indicating limited regeneration after canopy closure and a high mortality rate among cohorts. The relative dominance (basal area) generally declined with distance from the channel, but was high on some older plots (100+ years) that included large individuals that established on new point bar surfaces. Black willow and cottonwood also established on newly created surfaces. They were infrequent compared to silver maple and rarely occurred on the oldest plots.

Green ash and water hickory, which were absent on sites dominated by young silver maple stands, frequently established on older surfaces. Densities were highly variable among transects and there were no consistent trends that could be related to surface age (Table 6). However, the presence of large green ash and water hickory indicate successful establishment and size-class recruitment in the understory of the early colonizing species. In contrast, sugarberry and swamp privet were the most frequent understory species. Swamp privet colonized newly created surfaces, whereas sugarberry usually established on older surfaces that were already occupied by mature silver maple. Their relative densities, in some cases, exceeded that of green ash and water hickory.

Table 6
Number of Individuals and Dominance of the Most Common Species on Contiguous
Point Bar Transect Plots*

	Plots							
	1	2	3	4	5	6	7	8
Transect 1								
<i>Acer</i>	67 (98)	28 (58)	15 (40)	4 (27)	2 (18)	1 (3)	2 (13)	5 (45)
<i>Populus</i>		2 (37)	3 (53)					
<i>Salix</i>	1 (5)				1 (8)			
<i>Forestiera</i>	3 (2)		1 (<1)	6 (14)	3 (5)	3 (3)	2 (2)	1 (7)
<i>Fraxinus</i>			5 (20)	3 (33)	5 (5)	3 (10)	3 (47)	3 (14)
<i>Carya</i>				4 (3)	6 (29)	7 (81)	1 (18)	
<i>Celtis</i>				4 (12)	8 (7)	3 (2)	5 (15)	9 (24)
Transect 2								
<i>Acer</i>	96 (57)	24 (72)	28 (42)	23 (47)	17 (31)	10 (67)	15 (83)	3 (54)
<i>Populus</i>	1 (3)		2 (57)		1 (35)			
<i>Salix</i>	6 (35)			3 (17)	3 (34)			1 (32)
<i>Forestiera</i>		2 (3)				5 (28)	3 (4)	1 (<1)
<i>Fraxinus</i>			1 (<1)				1 (9)	4 (14)
<i>Carya</i>						1 (5)		
<i>Celtis</i>		1 (11)	2 (<1)				1 (4)	
Transect 3								
<i>Acer</i>	64 (26)	20 (22)	9 (46)	1 (6)	2 (12)			
<i>Populus</i>		3 (39)						
<i>Salix</i>	24 (74)	4 (33)	3 (43)	3 (47)				
<i>Forestiera</i>		1 (<1)						
<i>Fraxinus</i>			3 (4)	4 (17)	2 (53)			
<i>Carya</i>				2 (13)				
<i>Celtis</i>			9 (4)	17 (11)	18 (30)			
Transect 4								
<i>Acer</i>	99 (98)	21 (77)		4 (18)				
<i>Populus</i>			4 (88)	1 (53)				
<i>Salix</i>		1 (19)						
<i>Forestiera</i>	1 (2)	2 (2)	15 (4)	8 (5)				
<i>Fraxinus</i>		1 (2)		4 (12)				
<i>Carya</i>				1 (1)				
<i>Celtis</i>			8 (6)	9 (11)				

* Plots are 20 x 20 m. Plot 1 is adjacent to the channel, Plots 2-8 are on progressively older surfaces. Relative dominance (percent) based on basal area is in parentheses. Other species occurring infrequently in the transect plots were *Platanus occidentalis*, *Planera aquatica*, and *Gleditsia aquatica*.

5 Discussion

Channel migration is the primary mechanism for the regeneration of many floodplain species along the lower Hatchie River. New surfaces created by the filling in of oxbows and point bar deposition are rapidly colonized. Annual flooding of these sites and high rates of sedimentation allow only a small number of opportunistic species to establish successfully.

The establishment of terrestrial vegetation in abandoned channels is determined primarily by hydrologic conditions. Young oxbows typically hold water throughout the year, limiting colonization to the most flood-tolerant species, baldcypress and black willow, that only establish at the lake margins. Establishment at the center of the abandoned channel occurs after deposition of sediment and organic debris creates new surfaces that are exposed during low water levels. Baldcypress seeds are spread by floodwater, but will only germinate after deposition on exposed surfaces (Demaree 1932; Schneider and Sharitz 1988). Seedling survival depends on growth to sufficient height so that in later years they will not be completely submerged for long periods of time (Demaree 1932). Shelford (1954) suggested that this only occurs if successive drought years follow establishment. The frequent and prolonged inundation of baldcypress habitats makes these sites unsuitable for colonization by most other terrestrial species. The exception is black willow which typically colonizes new surfaces in alluvial habitats (Hosner and

Minckler 1960; Mcleod and McPherson 1973; Klimas 1988). Less flood-tolerant species begin to establish as deposition raises surfaces and reduces the frequency and duration of flooding. The reproductive success of later-arriving species depends on at least a moderate tolerance to frequent flooding and sediment deposition, which buries the lower tree bole, and the ability to maintain themselves beneath a baldcypress or black willow canopy.

Baldcypress and black willow are shade intolerant and regeneration of both species is discontinuous after the development of a forest canopy. Black willow grows faster than baldcypress and may dominate the abandoned channel in early succession. However, it is short-lived, and there is a rapid transition to baldcypress dominance. Baldcypress seeds are continually dispersed into the old channels where many first-year seedlings are found, but few seedlings survive after the development of a forest canopy and therefore regeneration is discontinuous. Although it has been noted that baldcypress is moderately shade tolerant (Fowells 1965), the results of this investigation are consistent with the findings of other studies, including that of Demaree (1932) who noted that in the St. Francis River basin in Arkansas, few seedlings that establish in shade would live into the second year (cf. Dunn and Sharitz 1987). Because of shade intolerance, the age range of baldcypress is no greater than the period of time from the creation of the oxbow and its initial coloniza-

tion until development of a continuous forest canopy, probably 200 to 300 years later. Baldcypress longevity exceeds that of most other species within its range (Stahle, Cleaveland, and Hehr 1985; 1988), and it will likely dominate the abandoned channels for several centuries. However, baldcypress stands begin to decline within 400 to 500 years of initial establishment, and they are rarely found on considerably older surfaces.

Early forest succession on point bars of the lower Hatchie River is considerably different than on abandoned channels. Among the early oxbow dominants, baldcypress rarely occurs on point bars, whereas black willow will occasionally establish, although not in large numbers. Silver maple is the only species that rapidly establishes on newly formed surfaces. Silver maple produces large amounts of seeds almost every

year that are disseminated by wind and water, and therefore, is likely to be among the first terrestrial species to establish. Rapid seedling growth reduces the probability of submersion during flooding that is common most years, and that likely inhibits successful establishment of other trees. The high reproductive success of silver maple is limited primarily to young surfaces. Cottonwood is the only other early colonizing species on point bars that occurs on more than an occasional basis. Slower growing, shade-tolerant species establish on the older surfaces, often under a dense forest canopy. Among these are green ash and water hickory, which also occurred in the baldcypress understory in meander scars. Both species can tolerate long periods of suppression. However, because of their size and longevity, they are likely to eventually share canopy dominance.

6 Conclusions

Terrestrial vegetation initially establishes within the active meander belt of the lower Hatchie River after erosion of the outer concave banks destroys previously existing stands and downstream deposition creates new surfaces. The early colonizing species on abandoned channels and point bars are those with similar reproductive and ecological characteristics: regular seed production, wind- or water-dispersed seeds, fast growth rates, high flood tolerance, and shade intolerance. Environmental conditions no longer favor the establishment of these species after a dense canopy cover develops. Therefore, with the exception of silver maple, which occurs in a variety of habitats, the early colonizing species (including baldcypress, black willow, and cottonwood) occur infrequently on older surfaces.

Channel migration is the major determinant of landscape and biotic diversity in alluvial habitats of the Southeastern Coastal Plain. Meander features at different stages of geomorphic development support plant communities at corresponding successional stages. Channel movement and the creation of oxbows will maintain the early colonizers

within the meander belt. However, the continuing development of these communities is threatened by channelization, which is common in the Southeastern Coastal Plain. Maintenance of a straightened channel excludes the formation of oxbows and point bars, which is the primary regeneration mechanism for some species.

Based on this investigation, stabilization of the Hatchie River would lead to a decline of vegetation diversity in associated alluvial habitats. Without channel migration, silver-maple-dominated point bar communities would largely disappear in less than 200 years. Baldcypress-dominated meander scar communities would no longer develop. Assuming sedimentation and baldcypress colonization rates are unchanged in existing oxbows, the unique meander scar baldcypress communities would decline over a period of 400 to 500 years, and be replaced by other more common forest types. Reduction or elimination of channel migration and the development of new surfaces would eventually reduce biotic diversity within the Hatchie River floodplain.

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Appendix A: Exact Probability Test

This exact probability test is based on a comparison of the observed distribution of trees to the total number of combinations of tree distances.

Tree distances were discretized as follows: Trees were located in 2-m-wide contiguous columns that were parallel to the channel banks. If a tree was in the column 0-2 m from the bank, its distance was 1; if 2-4 m, its distance was 2; etc. The maximum distance from the bank (N) is the middle of the former channel. When determining the probability of random center channel clustering, the distance is measured from the channel center.

The total number of combinations of distributing the k tree of a sample in up to N possible distances is given by Ross (1976):¹

$$\binom{N + k - 1}{k}$$

If each tree in a sample of k trees is at a distance d_i from the bank ($i=1,2,\dots,k$), the

total possible number of combinations of distances at the sample distances or closer to the bank can be calculated as:

$$\sum_{n_1=1}^{d_1} \sum_{n_2=n_1}^{d_2} \dots \sum_{n_k=n_{k-1}}^{d_k} (d_k - n_k + 1)$$

$$d_1 \leq d_2 \leq \dots \leq d_k$$

Assuming a tree has an equal chance of occurring at any of the N distances, the probability (P) of obtaining a given sample of distances of k trees or one closer to the bank is given by:

$$P = \frac{\sum_{n_1=1}^{d_1} \sum_{n_2=n_1}^{d_2} \dots \sum_{n_k=n_{k-1}}^{d_k} (d_k - n_k + 1)}{\binom{N + k - 1}{k}}$$

$$d_1 \leq d_2 \leq \dots \leq d_k$$

¹ See References at the end of the main text.